

# Phylogenetic relationships and taxonomic status of the endemic Socorro Warbler (*Setophaga pitiayumi graysoni*)

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**Abstract** The Socorro Warbler (*Setophaga pitiayumi graysoni*) is currently classified as a subspecies of the Tropical Parula. This bird is endemic to Socorro Island, and due to the island's distance from mainland Mexico and likely low levels of gene flow for this non-migratory species, we expected this form to exhibit significant divergence from its mainland counterparts. Here, we analyzed the phylogenetic position of the Socorro Warbler and examined its taxonomic status. Using blood samples from four individual Socorro Warblers, we performed phylogenetic analyses using the nuclear genes rhodopsin intron 1 (RDPSN) and transforming growth factor beta-2 (TGFB2), and the mitochondrial genes ATPase and cytochrome *b*. Bayesian inference, maximum-likelihood, and maximum parsimony analyses were employed to determine the genetic relationship of the Socorro Warbler to its mainland counterparts. Results reveal significant genetic divergence and a basal position of the Socorro Warbler relative to its mainland counterparts. Based on its distinct phylogenetic placement and geographical isolation, we recommend returning the Socorro Warbler to its original specific status, *Setophaga graysoni*, based on its taxonomic history. This case illustrates the importance of preserving island habitats to save unique island biodiversity that otherwise could pass unnoticed.

**Keywords** Socorro Warbler · *Setophaga pitiayumi graysoni* · Tropical Parula · Northern Parula · Cryptic species · Socorro island · Revillagigedo Archipelago

## Zusammenfassung

**Phylogenetische Beziehung und taxonomischer Status des endemischen Elfenwaldsängers von Socorro (*Setophaga pitiayumi graysoni*)**

Der Elfenwaldsänger von Socorro wird zur Zeit als Unterart des auf dem Festland vorkommenden Elfenwaldsängers klassifiziert. Dieser Vogel ist endemisch auf Socorro, und aufgrund der Entfernung der Insel vom mexikanischen Festland und vermutlich geringem genetischen Austausch dieser nicht-ziehenden Art, erwarteten wir, dass diese Form eine signifikante Abweichung zeigen würde von ihrem Gegenpart auf dem Festland. Hier analysierten wir die phylogenetische Position des endemischen Elfenwaldsängers und untersuchten seinen taxonomischen Status. Mit Blutproben von vier verschiedenen endemischen Elfenwaldsängern führten wir phylogenetische Analysen durch am Rhodopsin Intron 1 (RDPSN), dem transforming growth factor beta-2 (TGFB2) und den mitochondrialen Genen ATPase und Cytochrom *b*. Bayes'sche, Maximum Likelihood und Maximum Parsimony Analysen wurden durchgeführt, um die genetische Beziehung zwischen dem endemischen Elfenwaldsänger und seinem Gegenpart vom Festland festzustellen. Die Ergebnisse legen eine signifikante genetische Abweichung und eine basale Stellung des endemischen Elfenwaldsängers im Verhältnis zu seinem Gegenpart vom Festland offen. Aufgrund seiner deutlichen phylogenetischen Stellung, seiner geographischen Isolation und taxonomischen Geschichte, empfehlen wir, den ursprünglichen Art-Status

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des endemischen Elfenwaldsängers als *Setophaga graysoni* wiederherzustellen. Dieser Fall illustriert, wie wichtig der Erhalt von Inselhabitaten ist, um eine einzigartige Insel-Biodiversität zu schützen, die anderenfalls unbemerkt bleiben könnte.

## Introduction

The Socorro Warbler (*Setophaga pitiayumi graysoni*) is endemic to Socorro Island, which is located approximately 700 km west of Manzanillo, Mexico, and is the largest of the four Revillagigedo Islands with an approximate area of 132 km<sup>2</sup> (Martínez-Gómez and Curry 1996). The island is recognized for its high levels of endemism (Brattstrom 1990). Recently, after a thorough revision of genetic affinities of the wood warblers, the genus was changed from *Parula* to *Setophaga*, (Lovette et al. 2010; Chesser et al. 2011). Historically, wood warblers have served as an excellent system for ecological, evolutionary and behavioral studies (MacArthur 1958; Morse 1970; Shutler and Weatherhead 1990; Price et al. 2000; Martin and Martin 2001; Klein et al. 2004; Escalante et al. 2009; Lovette et al. 2010).

The Socorro Warbler was first collected by Grayson (1871) and was originally described as a distinct species (*Compothlypis graysoni*) by Ridgway (1887). Although its specific status was recognized by various taxonomic authorities (e.g., Ridgway 1902; McLellan 1926; American Ornithologists' Union 1957; Friedmann et al. 1957), Hellmayr (1935) could not see “anything but a strongly marked race” of the Tropical Parula. He was followed by others, and the subspecific status of the Socorro Warbler became widely accepted (Blake 1953; Brattstrom and Howell 1956; American Ornithologists' Union 1983). The Tropical Parula is a small passerine bird that breeds from the lower Rio Grande in Texas, USA, to La Plata in Argentina (Chapman 1925; Regelski and Moldenhauer 2012); currently 14 subspecies are recognized (Chesser et al. 2011; Regelski and Moldenhauer 2012). The Socorro Warbler has plumage that resembles juvenile Northern Parulas (*Setophaga americana*) lacking the ocular ring, or the continental female *Setophaga pitiayumi nigrilora* without a black facial mask. Nonetheless, some Socorro Warblers do possess a black facial mask (Baptista and Martínez-Gómez 2002). The Socorro Warbler has two primary song types as do the Tropical and Northern Parulas; however, their structure resembles those of Tropical Parulas of Western Mexico (Baptista and Martínez-Gómez 2002; Moldenhauer and Regelski 2012; Regelski and Moldenhauer 2012). Thus, plumage and song suggest a closer relationship between the Socorro Warbler and the Tropical Parula.

It has been proposed that, under phylogenetic and evolutionary species concepts, many island forms and subspecies should be recognized as distinct species (Peterson and Navarro-Sigüenza 1999; Navarro-Sigüenza and Peterson 2004). Recent studies indicate that several bird species on Socorro Island show marked genetic divergence from their mainland counterparts. Such is the case for the Socorro Dove (*Zenaida graysoni*; Johnson and Clayton 2000), the Socorro Mockingbird (*Mimus graysoni*; Barber et al. 2004), and the Socorro Wren (*Troglodytes sissonii*; Martínez-Gómez et al. 2005). Those species also show a basal phylogenetic placement relative to their mainland relatives. Thus, we predicted that the Socorro Warbler would show significant genetic divergence as do the other endemic land birds of Socorro Island. To evaluate this hypothesis, we conducted molecular analyses of mitochondrial and nuclear genes extracted from blood samples to infer phylogenetic reconstructions and determine the relationships between the Socorro Warbler and the mainland Tropical Parula.

## Methods

Total cellular DNA was extracted from blood tissue using the Animal Tissue Wizard SV purification kit (Promega, Madison, WI, USA) with Promega's recommended procedures. We used Polymerase Chain Reaction (PCR) in order to amplify two mitochondrial genes (ATPase subunits 8 and 6, cytochrome *b*) and two nuclear genes (rhodopsin intron 1, transforming growth factor beta-2 intron 5) from four individuals sampled at Socorro Island during the summer of 2011.

The primer set CO2GQL and CO3HMH was used to amplify a region that encompassed the ATPase 8 and 6 subunit genes (Hunt et al. 2001). The ATPase 8 and 6 subunit PCR reactions were processed with the following thermal cycler profile: denaturation at 94 °C for 3 min and 25 cycles of 94 °C for 45 s, annealing at 54 °C for 45 s, extension at 72 °C for 1 min, followed by a final extension at 72 °C for 5 min (Hunt et al. 2001). The cytochrome *b* gene was amplified by using the primers L14851 and H16065 (Randi 1996; Kornegay et al. 1993), and then processed using the following thermal cycler profile: denaturation for 1 min at 93 °C, annealing for 1 min at 50 °C and extension for 3 min at 72 °C for 30–35 cycles (Kornegay et al. 1993).

The rhodopsin intron 1 (RDPSN) nuclear gene was amplified using the RDPSN-F and RDPSN-R primers (Primmer et al. 2002). The rhodopsin PCR was processed using the following thermal cycler profile: denaturation at 94 °C for 2 min and 25 cycles of 95 °C for 30 s, annealing at 56 °C for 30 s, extension at 72 °C for 45 s, followed by a

**Table 1** Taxa used in the study in this study

Taxon	Name	Locality	ATPase	Cyt b	TGFB2	RDPSN
<i>Cardellina pusilla</i>	Wilson's Warbler	USA: Washington St., Wahkiakum County, Cathlamet	GU932129	GU932416	GU932492	GU932575
<i>Cardellina rubrifrons</i>	Red-faced Warbler	USA: Arizona	AF382987	AF383026	GU932488	GU932571
<i>Geothlypis tolmiei</i>	MacGillivray's Warbler	USA: Washington	AF382990	AF383029	GU932471	GU932554
<i>Geothlypis trichas</i>	Common Yellowthroat	Jamaica: St. Andrew Parish	AF382964	AF383003	GU932474	GU932557
<i>Mniotilta varia</i>	Black-and-white Warbler	Jamaica: St. Andrew Parish	AF382967	AF383006	GU932426	GU932509
<i>Myiothlypis conspicillatus</i>	White-lored Warbler	Colombia	GU932060	GU932380	GU932441	GU932530
<i>Myiothlypis flaveolus</i>	Flavescent Warbler	Boliva: Santa Cruz Department	AF382955	AF382994	GU932450	GU932533
<i>Oreothlypis gutturalis</i>	Flame-throated Warbler	Panama: Chiriqui Province, Boquete	GU932041	GU932363	GU932428	GU932511
<i>Oreothlypis luciae</i>	Lucy's Warbler	USA: Arizona, Cochise County	GU932132	GU932419	GU932495	GU932578
<i>Parkesia noveboracensis</i>	Northern Waterthrush	Honduras: Cochino Pequeno	AF382962	EU325772	GU932432	GU932515
<i>Protonotaria citrea</i>	Prothonotary Warbler	USA: Louisiana	AF382991	AF383030	GU932427	GU932510
<i>Seiurus aurocapilla</i>	Ovenbird	Jamaica: Westmoreland Parish	AF382968	GU932365	GU932430	GU932513
<i>Setophaga pititayumi graysoni</i>	Socorro Warbler	Mexico: Socorro Island	KF278958	KF278959	KF278961	KF278960
<i>Setophaga adelaidae</i>	Adelaide's Warbler	Saint Lucia: Babonneau, Anse Sorciere	GU932073	GU932390	GU932459	GU932543
<i>Setophaga americana</i>	Northern Parula	Jamaica: St. Elizabeth Parish	AF256480	AF256503	EU815818	EU815794
<i>Setophaga angelae</i>	Elfin-woods Warbler	Puerto Rico: Maricao State Forest	GU932074	GU932391	GU932461	GU932544
<i>Setophaga caerulescens</i>	Black-throated Blue Warbler	Jamaica: St. Andrews Parish, John Crow Nat. Park	GU932075	EU815674	EU815798	EU815774
<i>Setophaga castanea</i>	Bay-breasted Warbler	Unknown	AY650183	EU815675	EU815799	EU815775
<i>Setophaga cerulea</i>	Cerulean Warbler	USA: Louisiana St., Cameron Parish	GU932077	EU815676	EU815800	EU815776
<i>Setophaga coronata</i>	Yellow-rumped Warbler	Canada	AF140396	EU815677	EU815801	EU815777
<i>Setophaga discolor</i>	Prairie Warbler	Unknown	AY650214	AY216830	EU815802	EU815778
<i>Setophaga dominica</i>	Yellow-throated Warbler	USA: Louisiana St., Cameron Parish	GU932081	AY216838	EU815803	EU815779
<i>Setophaga fusca</i>	Blackburnian Warbler	Ecuador: Prov. Esmeraldas	GU932086	AY340208	EU815804	EU815780
<i>Setophaga graciae</i>	Grace's Warbler	USA: Arizona, Santa Cruz County	GU932087	EU815680	EU815805	EU815781
<i>Setophaga kirtlandii</i>	Kirtland's Warbler	United States	EU815661	EU815681	EU815806	EU815782
<i>Setophaga magnolia</i>	Magnolia Warbler	USA: New York St., Monroe County	GU932089	EU815682	EU815807	EU815783
<i>Setophaga nigrescens</i>	Black-throated Grey Warbler	USA: Washington St., Lewis County	GU932090	EU815683	EU815808	EU815784
<i>Setophaga occidentalis</i>	Hermit Warbler	USA: California St., Sierra County	GU932091	EU815684	EU815809	EU815785
<i>Setophaga palmarum</i>	Palm Warbler	USA: California St., San Bernardino County	GU932092	EU815685	EU815810	EU815786
<i>Setophaga pensylvanica</i>	Chestnut-sided Warbler	USA: New York St., Tompkins County	GU932093	EU815686	EU815811	EU815787
<i>Setophaga petechia</i>	Mangrove Warbler	Antigua and Barbuda: Barbuda	AF382957	EU815687	EU815812	EU815788
<i>Setophaga pharetra</i>	Arrowhead Warbler	Jamaica: St. Andrews Parish, John Crow Nat. Park	GU932095	GU932393	GU932463	GU932546
<i>Setophaga pinus</i>	Pine Warbler	USA: New Jersey	AF382988	AF383027	EU815813	EU815789
<i>Setophaga pititayumi</i>	Tropical Parula	Trinidad: Chacachacare Island	AF256484	AF256509	EU815819	EU815795
<i>Setophaga pityophila</i>	Olive-capped Warbler	Bahamas: Abaco Island	GU932097	GU932394	GU932464	GU932547
<i>Setophaga plumbea</i>	Plumbeous Warbler	Dominica: Springfield	GU932098	GU932395	GU932465	GU932548

**Table 1** continued

Taxon	Name	Locality	ATPase	Cyt b	TGFB2	RDPSN
<i>Setophaga ruticilla</i>	American Redstart	Unknown	AY650182	EU815694	EU815820	EU815796
<i>Setophaga striata</i>	Blackpoll Warbler	United States: Bucks City, Pennsylvania	EU815663	EU815688	EU815814	EU815790
<i>Setophaga tigrina</i>	Cape May Warbler	Unknown	AY650191	AF256505	EU815815	EU815791
<i>Setophaga townsendi</i>	Townsend's Warbler	USA: Washington St., Pend Oreille County	GU932101	EU815690	EU815816	EU815792
<i>Setophaga virens</i>	Black-throated Green Warbler	Unknown	AY650189	EU325770	EU815817	EU815793
<i>Setophaga vitellina</i>	Vitelline Warbler	Cayman Islands	AY481610	GU932396	GU932466	GU932549
<i>Vermivora cyanoptera</i>	Blue-winged Warbler	USA: New York St., Tompkins County	GU932047	GU932369	GU932434	GU932517

final extension at 72 °C for 5 min. The second nuclear gene, transforming growth factor beta-2 (TGFB2), was amplified with the TGFB-F and TGFB2-R primers and the following thermal cycler profile: denaturation at 94 °C for 2 min and 35 cycles of 95 °C for 30 s, annealing at 65 °C for 30 s, extension at 72 °C for 45 s, followed by a final extension at 72 °C for 5 min (Primmer et al. 2002). PCR products were run on 1.8 % agarose gels, followed by ethidium bromide staining for UV confirmation of positive results. After detection of positive PCR product through gel electrophoresis, products were sequenced using a BigDye [R] v.3.1 sequencing kit; (Applied Biosystems, Carlsbad, CA) on an ABI PRISM 3100<sup>TM</sup> sequencer (Loiseau et al. 2011).

To phylogenetically characterize the Socorro Warbler, the mitochondrial and nuclear sequences obtained from four individuals collected on Socorro Island were aligned to comparable published GenBank sequences of all four genes (Table 1). Sequences were aligned using Sequencher 4.9 and ClustalX 2.1 (Loiseau et al. 2011). Phylogenetic analyses of the individual genes yielded trees with similar topologies, but lacked resolution at the relevant nodes. In order to increase resolution and to improve accuracy of phylogenetic inference, we employed a concatenation approach with the mitochondrial and nuclear genes (e.g., Rosenberg and Kumar 2001). A non-partitioned analysis was used with the concatenated genes as it has been shown that it produces equivalent or better accuracy at inferring correct nodes when compared to a consensus approach using a partitioned analysis (Gadagkar et al. 2005). Moreover, Lovette et al. (2010) reported that many of their analyses failed to converge on a supercomputer cluster using a consensus approach with a partitioned analysis. Consequently, we did not attempt a partitioned analysis because our aim was not to recreate the comprehensive phylogeny of the wood-warblers (Lovette et al. 2010), but to examine phylogenetic relationships of the Socorro Warbler and its closest relatives.

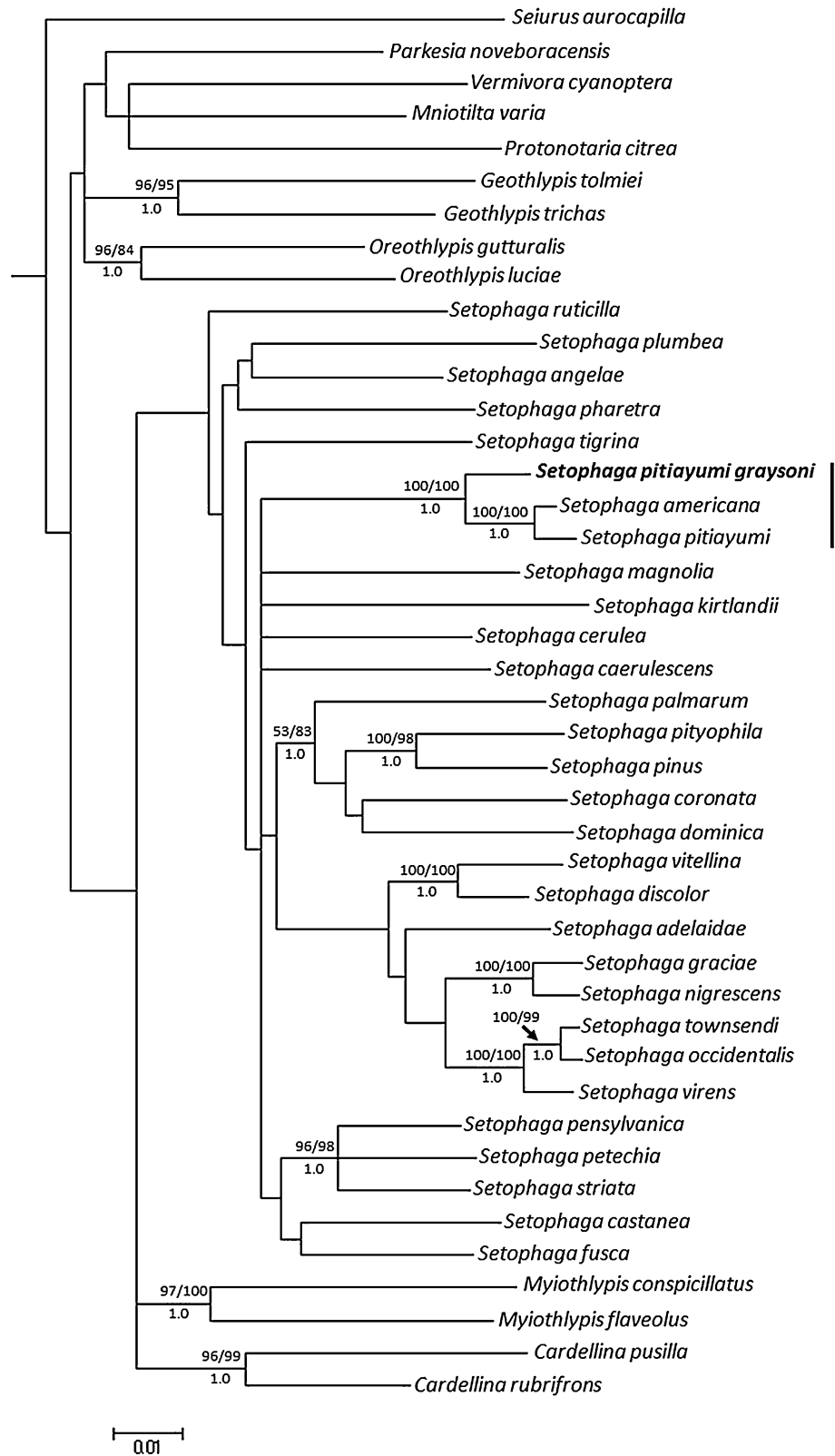
Concatenated sequences were analyzed using Bayesian inference (BI) with an enforced topology to maintain

known relationships, maximum-likelihood (ML) analysis, and maximum parsimony (MP). BI analysis was conducted with MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003), with models generated by pre-analysis in ModelTest 2.3 (Nylander et al. 2004) using Akaike information criterion (AIC) scores (Posada and Buckley 2004). The clade containing the Socorro Warbler and its relatives was not constrained in the BI analysis. We analyzed sequences with MrBayes using a GTR+G+I model with the Markov Chain Monte Carlo (MCMC) algorithm and 10 million generations at a sample frequency of 200. ML analyses were performed with MEGA 5 (v.5.1.0) using the GTR+G+I with 1,000 bootstrap replications. MP analyses were also conducted in MEGA 5 using 1,000 bootstrap replications (Tamura et al. 2011). A maximum likelihood ratio test selected the following model:  $-\ln L = 17,955.884$ , substitution with all equal rates, base frequencies  $A = 0.264$ ,  $C = 0.301$ ,  $G = 0.163$ ,  $T = 0.272$ , gamma distribution shape parameter = 0.49, and invariant sites distribution parameter 0.56. These parameters correspond to the General Time Reversal model with gamma and invariant sites distributions (GTR+G+I). Sequence divergence was calculated solely from cytochrome *b* sequences using Kimura 2-parameter settings in MEGA 5 (Kimura 1980).

## Results

The Socorro Warbler concatenated sequence was 3,390 bp in length of which 2,473 were constant, 317 autapomorphic and 596 phylogenetically informative. Sequences from the four Socorro Warblers were 100 % identical in the RDSPN, TGFB2 and Cyt *b* genes. Two individuals differed in the ATPase subunits 8 and 6 gene by 3 bp. We were able to obtain sequences from all 4 individuals with the RDPSN and TGFB2 genes; however, only 3 of the Cyt *b* and 2 of the ATPase subunits 8 and 6 sequences were recoverable.

**Fig. 1** The results of ML, MP and BI approaches to determine the phylogenetic position of the Socorro Warbler *Setophaga pitiayumi graysoni* using a 3,390-bp concatenated sequence of ATPases, *Cyt b*, TGFB2 and RDPSN. Overall tree topology and branch lengths implemented enforced BI analysis to conform to that of the more comprehensive phylogeny of Lovette et al. (2010). The clade containing the Socorro Warbler was not constrained in the BI analysis. The numbers above the lines are the nodal support values for maximum likelihood and maximum parsimony (ML/MP) and the numbers below the lines indicate Bayesian posterior probabilities



Phylogenetic relationships of the Socorro Warbler to the Tropical Parula and the Northern Parula are depicted in Fig. 1. The tree reveals significant genetic divergence

between the Socorro Warbler and Tropical Parula and a basal position of the Socorro Warbler to both the Northern Parula and the Tropical Parula. Analyses using the

**Table 2** Sequence divergence (in percentage) derived from Cyt *b* sequences of the Socorro Warbler *Setophaga pitiayumi graysoni*, Tropical Parula *S. pitiayumi*, Northern Parula *S. americana*, Prairie Warbler *S. discolor* and the Cape May Warbler *S. tigrina*

Taxon	1	2	3	4	5
1 <i>S. pitiayumi graysoni</i>	0				
2 <i>S. pitiayumi</i>	2.7	0			
3 <i>S. americana</i>	2.3	0.6	0		
4 <i>S. discolor</i>	6.5	7.3	7.5	0	
5 <i>S. tigrina</i>	6.1	7.7	7.9	6.7	0

The Kimura 2-parameter model was used to calculate sequence divergence

individual mitochondrial sequences (Cyt *b* and ATPase subunits 8 and 6) revealed a tree of similar topology to the concatenated sequences; nonetheless, strong nodal support became clear once nuclear genes were included (e.g., Zink and Barrowclough 2008). The three methods employed (BI, ML, MP) confirmed the monophyly of the clade containing the Socorro Warbler, the Tropical Parula and the Northern Parula with a strong nodal support of 100 % assessed via 1,000 bootstrap replicates. Genetic distances between the Socorro Warbler and the Northern Parula or Tropical Parula are 2.3 and 2.7 %, respectively; suggesting a closer relationship between the Socorro Warbler and the Northern Parula (Table 2).

## Discussion

It is noteworthy that the Northern Parula and Tropical Parula are considered distinct species with a genetic divergence of 0.6 %. while the Socorro Warbler is currently considered a subspecies of the Tropical Parula despite 2.7 % sequence divergence. A general molecular clock estimate for mitochondrial sequences of ca. 2 % per million years (e.g., Tarr and Fleischer 1993; Weir and Schluter 2008), would suggest a split between the Tropical Parula and its mainland counterparts of approximately 1.15 Ma. Divergence times of other terrestrial endemic land birds suggest that the Socorro Warbler arrived after the Socorro Wren *Troglodytes sissonii* (ca. 3 Ma; Martínez-Gómez et al. 2005). The Socorro Mockingbird *Mimus graysoni* (ca. 0.58–0.88 Ma; Barber et al. 2004; Lovette et al. 2012), and the Socorro Dove *Zenaida graysoni*; 0.45 Ma; Johnson and Clayton 2000) apparently arrived after the endemic warbler.

Generally, phenotypic characteristics of island forms experience enhanced genetic drift and selective pressures that produce species that can exploit novel niches (Barber et al. 2004). It has been observed that island birds can have

longer tarsi and bills, greater overall body size and dull plumage (Carlquist 1974; Grant 1965, 1968; Wright and Steadman 2012). Interestingly, plumage distinctiveness has not been fully achieved by the Socorro Warbler, and, in contrast, it has a plumage and vocalizations that resemble the Tropical Parula while genetically it is closer to the Northern Parula. This example shows how labile plumage characters and vocalizations can be. Notwithstanding, our findings strongly suggest that the Socorro Warbler should be treated as a distinct species based on the appreciable genetic distance and its basal placement.

Our contribution corroborates the proposition advanced by Peterson and Navarro-Sigüenza (1999) suggesting the evolutionary distinctiveness of island birds. The phylogenetic placement of the Socorro Warbler and other bird endemics of Socorro Island conform to that pattern. In fact, it has been recently found that other species previously considered subspecies based on morphology are in fact cryptic species that passed unnoticed until the advent of molecular techniques. This is the case of the Bahama Yellow-throated Warbler (*Setophaga flavescens*; McKay et al. 2010; Chesser et al. 2011) or the Guadalupe Junco (*Junco insularis*; Pau et al. 2013). We propose that the Socorro Warbler should be treated as a distinct species under the Phylogenetic Species Concept. An alternative approach, lumping the Socorro Warbler, Tropical Parula and Northern Parula as a single species would be less parsimonious in spite of known hybridization events reported for the last two species (Lovette and Bermingham 2001). Although treating the Tropical and Northern Parulas as one species different from the Socorro Warbler has not been proposed (e.g., American Ornithologists' Union 1998), the Tropical and Northern Parula were considered a superspecies at one point (Mayr and Short 1970). The example provided by the Socorro Warbler highlights the importance of studying the evolution of island avifaunas. Additional ecological and evolutionary studies on Socorro Island will help protect other cryptic and unnoticed species.

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## References

- American Ornithologists Union (1957) Checklist of North American birds, 5th edn. Port City, Baltimore
- American Ornithologists Union (1983) Checklist of North American birds, 6th edn. Allen, Lawrence
- American Ornithologists Union (1998) Checklist of North American birds, 7th edn. Allen, Lawrence
- Baptista LF, Martínez-Gómez JE (2002) La investigación bioacústica de las aves del Archipiélago de Revillagigedo: un reporte de avance. *Huitzil* 3:33–41
- Barber BR, Martínez-Gómez JE, Peterson AT (2004) Systematic position of the Socorro mockingbird *Mimodes graysoni*. *J Avian Biol* 35:195–198
- Blake ER (1953) Birds of Mexico. A guide for field identification. University of Chicago Press, Chicago
- Brattstrom BH (1990) Biogeography of the Islas Revillagigedo, Mexico. *J Biogeogr* 17:177–183
- Brattstrom BH, Howell TR (1956) The birds of the Revilla Gigedo islands, Mexico. *Condor* 58:107–120
- Carlquist S (1974) Island biology. Columbia University Press, New York
- Chapman FM (1925) The relationships and distribution of the warblers of the genus *Compsothlypis*: a contribution to the study of the origin of Andean bird life. *Auk* 42:193–208
- Chesser RT, Banks RC, Barker FK, Cicero C, Dunn JL, Kratter AW, Lovette IJ, Rasmussen PC, Remsen JV, Rising JD, Stotz DF, Winker K (2011) Fifty-second supplement to the American ornithologists' union check-list of North American Birds. *Auk* 128:600–613
- Escalante P, Márquez-Valdelamar L, Torre PDL, Lacleste JP, Klicka J (2009) Evolutionary history of a prominent North American warbler clade: the *oporonis*–*geothlypis* complex. *Mol Phylog Evol* 53:668–678
- Friedmann H, Griscom L, Moore RT (1957) Distributional check-list of the birds of Mexico Part II. *Pac Coast Avifauna* 33:1–436
- Gadagkar SR, Rosenberg MS, Kumar S (2005) Inferring species phylogenies from multiple genes: concatenated sequence tree versus consensus gene tree. *J Exp Zool* 304:64–74
- Grant PR (1965) Plumage and the evolution of birds on islands. *Syst Zool* 14:47–52
- Grant PR (1968) Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. *Syst Zool* 17:319–333
- Grayson AJ (1871) On the physical geography and natural history of the islands of the Tres Marias and of Socorro, off the western coast of Mexico. *Proc Boston Soc Nat Hist* 14:61–302
- Hellmayr CE (1935) Catalogue of birds of the Americas and the adjacent islands in the Field Museum of Natural History, Part VIII. Alaudidae, Hirundinidae, Motacillidae, Bombycillidae, Ptilonotidae, Dulidae, Vireonidae, Vireolaniidae, Cyclarhidae, Laniidae, Sturnidae, Coerebidae, Compsothlypidae. *Field Mus Nat Hist Zool Ser* 13:23–24
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: bayesian inference of phylogenetic trees. *Bioinformatics* 17:754–755
- Hunt JS, Bermingham E, Ricklefs RE (2001) Molecular systematics and biogeography of Antillean thrashers, tremblers, and mockingbirds (Aves: Mimidae). *Auk* 118:35–55
- Johnson KP, Clayton DH (2000) A molecular phylogeny of the dove genus *Zenaidra*: mitochondrial and nuclear DNA sequences. *Condor* 102:864–870
- Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J Mol Evol* 16:111–120
- Klein NK, Burns KJ, Hackett SJ, Griffiths CS (2004) Molecular phylogenetic relationships among the wood warblers (Parulidae) and historical biogeography in the Caribbean basin. *J Carib Ornithol* 17:3–17
- Kornegay J, Kocher TD, Williams LA, Wilson AC (1993) Pathways of lysozyme evolution inferred from the sequences of cytochrome b in birds. *J Mol Evol* 37:367–379
- Loiseau C, Harrigan RJ, Robert A, Bowie RC, Thomassen HA, Smith TB, Sehgal RN (2011) Host and habitat specialization of avian malaria in Africa. *Mol Ecol* 21:431–441
- Lovette IJ, Bermingham E (2001) A mitochondrial sequence-based phylogenetic analysis of Parula wood-warblers (Aves: Parulidae). *Auk* 118:211–215
- Lovette IJ, Pérez-Emán JL, Sullivan JP, Banks RC, Fiorentino I, Córdoba-Córdoba S, Echeverry-Galvis M, Barker FK, Burns KJ, Klicka J, Lanyon SM, Bermingham E (2010) A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves). *Mol Phylogenet Evol* 57:753–770
- Lovette IJ, Arbogast BS, Curry RL, Zink RM, Botero CA, Sullivan JP, Talaba AL, Harris RB, Rubenstein DR, Ricklefs RE, Bermingham E (2012) Phylogenetic relationships of the mockingbirds and thrashers (Aves: Mimidae). *Mol Phylogenet Evol* 63:219–229
- MacArthur RH (1958) Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599–619
- Martin PR, Martin TE (2001) Behavioral interactions between coexisting species: song playback experiments with wood warblers. *Ecology* 82:207–218
- Martínez-Gómez JE, Curry RL (1996) The conservation status of the Socorro Mockingbird *Mimodes graysoni* in 1993–1994. *Bird Conserv Int* 6:271–283
- Martínez-Gómez JE, Barber B, Peterson AT (2005) Phylogenetic position and generic placement of the Socorro wren *Thryomanes sissonii*. *Auk* 122:50–55
- Mayr E, Short LL (1970) Species taxa of North American birds. Publications of the Nuttall Ornithological Club 9
- McKay BD, Reynolds MJB, Hayes WK, Lee DS (2010) Evidence for the species status of the Bahama Yellow-Throated Warbler (*Dendroica* “*Dominica*” *flavescens*). *Auk* 127:932–939
- McLellan ME (1926) Expedition to the Revillagigedo islands, Mexico, in 1925, VI. The birds and mammals. *Proc Cal Acad Sci* 15:279–322
- Moldenhauer RR, Regelski DJ (2012) Northern Parula (*Setophaga americana*). The birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/215>
- Morse DM (1970) Ecological aspects of some mixed-species foraging flocks of birds. *Ecology* 40:119–168
- Navarro-Sigüenza AG, Peterson AT (2004) An alternative species taxonomy of the birds of Mexico. *Biota Neotrop* 4(n2):1–32 BN03504022004
- Nylander JA, Ronquist F, Huelsenbeck JP, Nieves-Aldrey JL (2004) Bayesian phylogenetic analysis of combined data. *Syst Biol* 53:47–67
- Pau A, Hernández Montoya J, Milá B (2013) Speciation on oceanic islands: rapid adaptive divergence vs. cryptic speciation in a Guadalupe Island songbird (Aves: *Junco*). *PLoS ONE* 8:1–12
- Peterson AT, Navarro-Sigüenza AG (1999) Alternate species concepts as bases for determining priority conservation areas. *Conserv Biol* 13:427–431
- Posada D, Buckley TR (2004) Model selection and model averaging in phylogenetics: advantages of akaike information criterion and bayesian approaches over likelihood ratio tests. *Syst Biol* 53:793–808

- Price T, Lovette IJ, Bermingham E, Gibbs HL, Richman AD (2000) The imprint of history on communities of North American and Asian warblers. *Am Nat* 156:354–367
- Primmer CR, Borge T, Lindell J, Saetre GP (2002) Single-nucleotide polymorphism characterization in species with limited available sequence information: high nucleotide diversity revealed in the avian genome. *Mol Ecol* 11:603–612
- Randi E (1996) A Mitochondrial cytochrome b phylogeny of the *Alectoris* partridges. *Mol Phylogenet Evol* 6:214–227
- Regelski DJ, Moldenhauer RR (2012) Tropical Parula (*Setophaga pitiayumi*). The birds of North America online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/293>
- Ridgway R (1887) A manual of North American birds. Lippincott, Philadelphia
- Ridgway R (1902) The birds of North and Middle America, Part II. *Bull US Nat Mus* 50:1–834
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574
- Rosenberg MS, Kumar S (2001) Incomplete taxon sampling is not a problem for phylogenetic inference. *Proc Natl Acad Sci USA* 98:10751–10756
- Shutler D, Weatherhead PJ (1990) Targets of sexual selection: song and plumage of wood warblers. *Evolution* 44:1967–1977
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol Biol Evol* 28:2731–2739
- Tarr CL, Fleischer RC (1993) Mitochondrial-DNA variation and evolutionary relationships in the *Amakihi* complex. *Auk* 110:825–831
- Weir JT, Schluter D (2008) Calibrating the avian molecular clock. *Mol Ecol* 17:2321–2328
- Wright NA, Steadman DW (2012) Insular avian adaptations on two Neotropical continental islands. *J Biogeogr* 39:1891–1899
- Zink RA, Barrowclough GF (2008) Mitochondrial DNA under siege in avian phylogeography. *Mol Ecol* 17:2107–2121